Taxonomic variation in larval mandibular structure in Palaearctic Notodontidae (Noctuoidea)

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Abstract. The mandibles of the 1st to 5th instar larvae of 61 species belonging to 32 genera of Palaeartic Notodontidae from Ukraine and Primorskii krai (Far East of Russia) were examined with the use of a scanning electron microscope. The characters of the mandibular margin, retinaculum and mandibular carina are discussed. A comparative morphological analysis is provided for all these structures. Apomorphic and plesiomorphic states of the different characters are argumented in relation to the different taxa. The results are compared to the recent classifications of Notodontidae.

Zusammenfassung. Die Mandibeln der ersten bis fünften Larvenstadien von 61 Arten und 32 Gattungen palärktischer Notodontidae aus der Ukraine und dem Primorski Krai in Russland sind rasterelektronenmirkoskopisch untersucht. Merkmale des Mandibelrandes, des Retinaculums und der Mandibelcarina werden diskutiert. Eine vergleichende morphologische Analyse wird für diese Merkmale gegeben. Die apomorphen und plesiomorphen Zustände der einzelnen Merkmale werden in Beziehung zu den einzelnen Taxa diskutiert. Die Ergebnisse werden mit rezenten Klassifikationen der Notodontidae verglichen.

Résumé. Les mandibules des chenilles de plusieurs Notodontidés paléarctiques ont été étudiés à l'aide du microscope électronique à balayage. L'étude est fondée sur les chenilles des stades I-V appartenant à 61 espèces de 32 genres provenant de l'Ukraine et de la Région d'Ussuri (au sud de l'Extrême est de la Russie). La morphologie des caractères tels que la marge mandibulaire, le retinaculum et la carène mandibulaire a été comparée. Une argumentation concernant les états de ces caractères en tant qu'apomorphies et plésiomorphies est fournie. Les récentes classifications des Notodontidés sont comparées en regard des résultats obtenus.

Introduction

The mandibles of final instar notodontid larvae have been described in certain publications (Godfrey 1984; Godfrey et al. 1989; Miller 1991), but our knowledge concerning other instars, particularly the morphological peculiarities of the first instar, is insufficient. Faunal coverage is also inadequate; most information treats notodontid species from North America (Weller 1987; Dockter 1993). This study is an attempt to, at least partly, close this gap.

Materials and Methods

This research is based on material that I have collected in Ukraine and Primorskii krai (Far East of Russia). Eggs were obtained from females captured in the field. Hatched larvae were reared to pupae. The epicrania left by caterpillars after moulting as well as fresh material stored in alcohol were studied. Mandibles were separated from the epicranium and then examined with a scanning electron microscope (SEM) as well as a binocular light microscope (MBS-9). The mandibular structures of 1st through 5th larval instars belonging to 61 notodontid species from the following genera were studied: *Euhampsonia* Dyar, *Furcula* Lamarck, *Uropyia* Staudinger, *Stauropus* Germar, *Cnethodonta* Staudinger, *Harpyia* Ochsenheimer, *Dicranura* Reichenbach, *Fentonia* Butler, *Drymonia* Hübner, *Notodonta* Ochsenheimer, *Peridea* Stephens, *Nerice*

Walker, *Semidonta* Staudinger, *Pheosia* Hübner, *Leucodonta* Staudinger, *Lophocosma* Staudinger, *Pheosiopsis* Bryk, *Shaka* Matsumura, *Pterostoma* Germar, *Ptilodon* Hübner, *Lophontosia* Staudinger, *Hagapteryx* Matsumura, *Allodonta* Staudinger, *Hexafrenum* Matsumura, *Epodonta* Matsumura, *Phalera* Hübner, *Spatalia* Hübner, *Gluphisia* Boisduval, *Pygaera* Ochsenheimer, *Gonoclostera* Butler, *Clostera* Samouelle and *Micromelalopha* Nagano. The taxonomic arrangement of these genera follows Schintlmeister (1989) (Table 1).

Results

Table 1 gives a summary of the distribution of the character states found during my investigations of the mandibular margin, retinaculum, and mandibular carina of the investigated Palaearctic genera of Notodontidae.

Mandibular margin. The presence of mandibles with a serrate cutting edge in the first larval instar, which then becomes smooth in the last instar, has been previously recorded (Weller 1987; Godfrey et al. 1989). Miller (1991) considered this smooth mandibular margin of Notodontidae to be an apomorphic character of the family.

The 1st instar mandibular margin in most species possesses 6 acutely-angled denticles. These are either narrow or broad and they vary in length. The middle denticles are the largest, while the 6th is usually indistinct (Fig. 1).

First instar larvae show taxonomic differences in mandibular edge structure. First of all, there is a trend toward smoothing out of the cutting edge. Thus, in most species the first instar mandibular edge shows 6 acutely-angled narrow denticles (*Hagapteryx*, *Phesiopsis*, *Furcula*, and others). Some species of Notodontinae have smooth, broad and more rounded denticles (e.g., *Pheosia*, *Phalera*, Fig. 2). In some taxa, the number of denticles is reduced to 4, the denticles are broad (perhaps due to fusion of separate denticles) and flattened. Thus, in genus *Cnethodonta* there are 4 large broad denticles (Fig. 3), while the denticles in species of *Stauropus* are almost indistinct (Fig. 4). Weller (1987: 189, fig. 2) recorded only 3 finger-like denticles for *Litodonta hydromeli* Harvey. Since the third denticle is broad, it is assumed to represent a fusion of two denticles.

My studies show that the mandibular margin of Notodontidae becomes smooth in the 2nd through 5th instars (Fig. 5). However, in some genera serrate mandibles do not completely disappear by the 2nd instar, but instead gradually disappear during subsequent instars, becoming absent by the final instar. For example, *Clostera*, *Gonoclostera, Pygaera, Micromelalopha*, and *Gluphisia* have 6 denticles in the 1st instar (Figs 6, 7) and retain 5 or 6 of them in the 2nd instar, though they become broader (Fig. 8). These genera have a smooth mandibular margin beginning in the 3rd instar.

In *Nerice* and *Dicranura*, 6 denticles persist in the 2nd instar. In *Nerice* they are short and rounded (Figs 9, 10) in the 2nd instar, but are expressed as 6 fused but distinct denticles in subsequent instars (Fig. 11). In *Dicranura*, the 2nd instar shows 5 or 6 indistinct denticles (Fig. 12). The mandibular margin in the 3rd instar is expressed as 5 fused less distinct denticles (Fig. 13), while the 4th instar mandibular edge is wavy (Fig. 14).

Tab. 1. Character states of the larval mandibles of Palaearctic Notodontidae.

Species	Mandibular margin			Retinaculum	Mandibular carina
	1st instar	2nd instar	3–5th instars		
Euhampsonia cristata (Butler)	6A	S	S	2 i, L	E
Euhampsonia splendida (Oberthür)	6A	S	S	2 i, L	E
Furcula furcula (Clerck)	6A	S	S	2 i, L	E
Furcula bicuspis (Borkhausen)	6A	S	S	2 i, L	E, M
Furcula bifida (Brahm)	6A	S	S	2 i, L	E
Uropyia meticulodina (Oberthür)	6A	S	S	2 i, H	E
Stauropus fagi (Linnaeus)	4B	S	S	1 i, L	E, M
Stauropus basalis Moore	4B	S	S	1 i, L	E
Cnethodonta grisescens Staudinger	4B	S	S	1 i, L	E, M
Harpyia milhauseri (Fabricius)	6A	S	S	2 i, L	E
Harpyia umbrosa (Staudinger)	6A	S	S	2 i, L	E
Dicranura ulmi (Denis & Schiffermüller)	6A	T	W**	3 i, H	M
Fentonia ocypete (Bremer)	6A	S	S	2 i, L	E
Drymonia dodonaea [Denis & Schiffermüller]	6A	S	S	2 i, L	E
Notodonta torva (Hübner)	6A	S	S	2 i, L	E
Notodonta dromedarius (Linnaeus)	6A	S	S	2 i, L	E
Notodonta dembowskii Oberthür	6A	S	SW	2 i, L	E
Notodonta tritophus phoebe (Siebert)	6A	S T	S	2 i, L	E
Notodonta ziczac (Linnaeus)	6A	S	S	2 i, L	E
Peridea anceps (Goeze)	6A	S	S	2 i, L	E
Peridea lativitta (Wileman)	6A	S	S	2 i, L	E
Peridea elzet Kiriakoff	6A	S	S	2 i, L	E
Peridea graeseri (Staudinger)	6A	S	S	2 i, L	E

Tab. 1. Continuation.

Species	Mandibular margin			Retinaculum	Mandibular carina
	1st instar	2nd instar	3–5th instars		
Peridea moltrechti (Oberthür)	6A	S	S	2 i, L	E
Peridea oberthueri (Staudinger)	6A	S	S	2 i, L	E
Nerice davidi Oberthür	6A	T	T	2 i, H	M
Nerice leechi Staudinger	6A	T	T	2 i, H	M
Semidonta biloba(Oberthür)	6A	S	S	2 i, L	E
Pheosia tremula (Clerck)	6B	S	S	2 i, L	E
Pheosia gnoma (Fabricius)	6B	ST	S	2 i, L	E, M
Pheosia rimosa Packard	6B	S	S	2 i, L	E
Leucodonta bicoloria (Den. & Schiffermüller)	6A	S	S	2 i,L	E
Lophocosma atriplaga Staudinger	6A	S	S	2 i, L	E
Pheosiopsis cinerea (Butler)	6A	S	S	2 i, L	E
Shaka atrovittatus (Bremer)	6A	S	S	2 i, L	E
Pterostoma palpina (Clerck)	6A	ST	S	2 i, L	E
Pterostoma sinicum Moore	6A	S	S	2 i, L	E
Pterostoma griseum (Bremer)	6A	S	S	2 i, L	E
Ptilodon capucina (Linnaeus)	6A	S	S	2 i, L	E, M
Ptilodon hoegei (Graeser)	6A	S	S	2 i, L	E
Ptilodon cucullina (Denis & Schiffermüller)	6A	S	S	2 i, L	E
Ptilodon ladislai (Oberthür)	6A	S	S	2 i, L	E
Lophontosia cuculus (Staudinger)	6A	S	S	2 i, L	E
Hagapteryx admirabilis (Staudinger)	6A	S	S	2 i, L	E
Allodonta plebeja (Oberthür)	6A	S	S	2 i, L	E, M
Hexafrenum leucodera (Staudinger)	6A	S	S	2 i, L	E, M

Tab. 1. Continuation.

Species	Mandibular margin			Retinaculum	Mandibular carina
	1st instar	2nd instar	3–5th instars		
Epodonta lineata (Oberthür)	6A	ST	SW	2 i, L	E
Phalera bucephala (Linnaeus)	6B	S	S	2 i, L H	M
Spatalia argentina (Denis & Schiffermüller)	6A	S	S	2 i,L	E
Spatalia doerriesi Graeser	6A	S	S	2 i, L	E
Spatalia plusiotis (Oberthür)	6A	S	S	2 i, L	E
Spatalia dives Oberthür	6A	S	S	2 i, L	E, M
Gluphisia crenata (Esper)***	6A	T	S	3–4 i, L	E
Pygaera timon (Hübner)	6A	T	S	4 i, L	M
Gonoclostera timoniorum (Bremer)	6A	T	S	2 i, L	E
Clostera curtula (Linnaeus)	6A	T	S	2 i, L	M
Clostera albosigma curtuloides (Erschoff)	6A	T	S	2 i, L	M
Clostera pigra (Hufnagel)	6A	T	S	2 i, L	M
Clostera anachoreta [Denis & Schiffermüller]	6A	T	S	2 i, L	M
Clostera anastomosis (Linnaeus)	6A	T	S	2 i, L	M
Micromelalopha troglodyta (Graeser)	6A	T	S	2 i, L	M

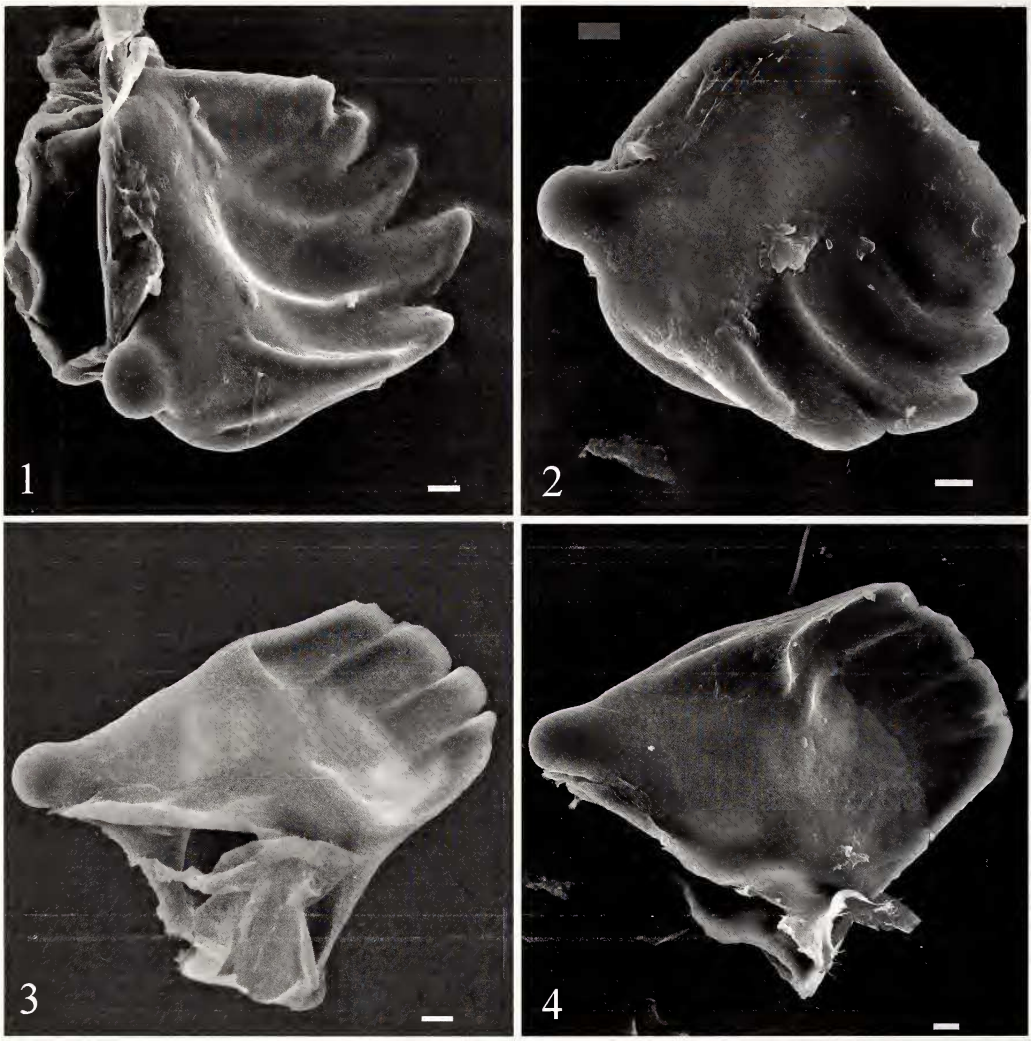
Mandibular margins with 6 acutely-angled narrow denticles (6A), with 6 broad, flattened denticles (6B), with 4 broad, flattened denticle (4B), smooth (S), toothed (T), or wavy (W).

Retinaculum flattened or with small projection (L) or with large, high comb (H). The presence of a retinaculum in the 1st instar (1i), in the 2nd instar (2i), in the 3rd instar (3i), in the 4th instar (4i).

Mandibular carina weakly expressed (E) or clearly expressed (M). Average situation between two extremes (ST, SW, EM).

** The mandibular margin in the 3rd instar is expressed as 5 fused, less distinct denticles, while the 4th instar mandibular edge is wavy.

*** did not have the 3rd instar larva and I do not know its characteristics.

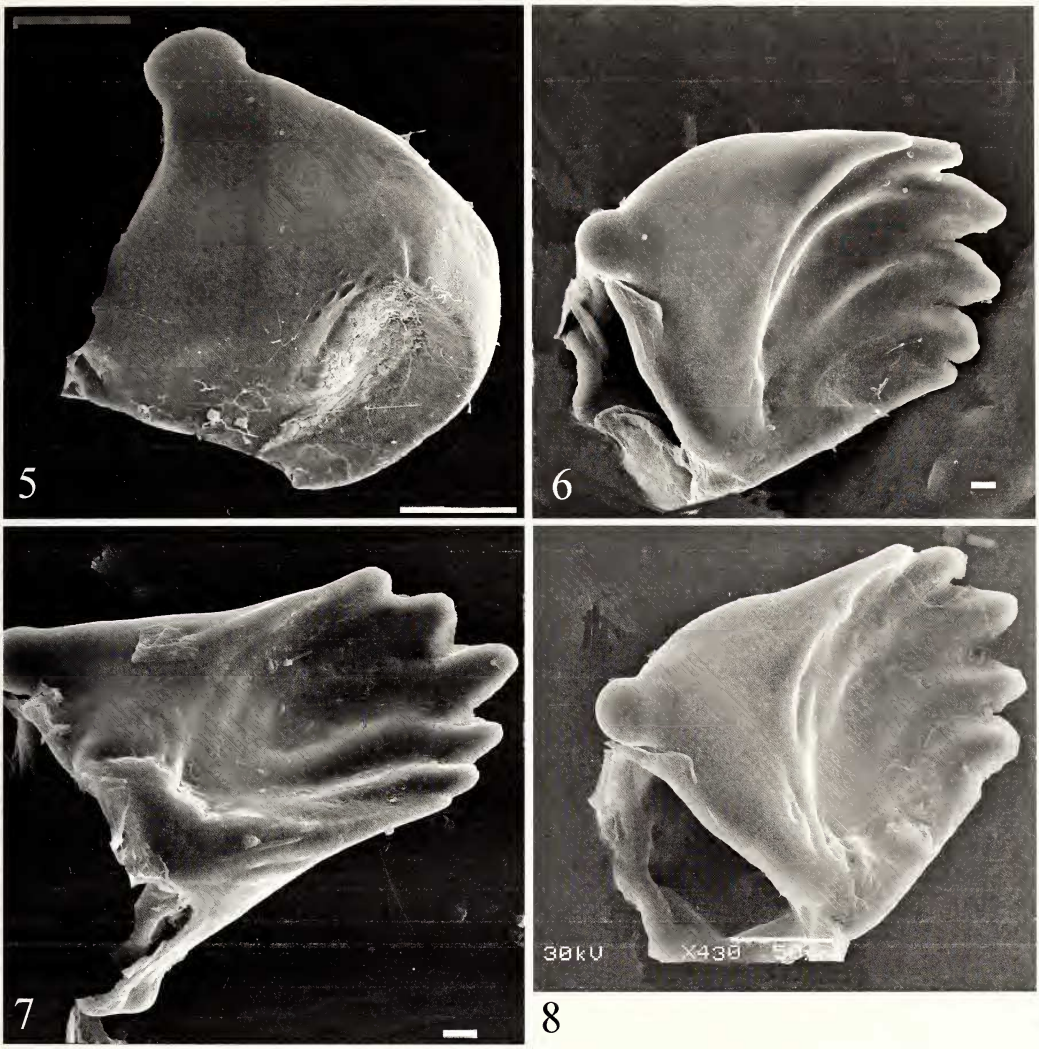


Figs 1–4. Oral surface of mandibles of 1st instar Notodontidae larvae. **1.** *Ptilodon hoegei* (left mandible, 600 ×). **2.** *Phalera bucephala* (left mandible, 720 ×). **3.** *Cnethodonta grisescens* (right mandible, 600 ×). **4.** *Stauropus fagi* (right mandible, 480 ×).

Dockter (1993: 37, 38, Fig. 8) pointed out that in 1st instar larvae of *Heterocampa guttivitta* Walker the "third and fourth teeth have flanges on the bases of their ventrolateral edges". My studies of 1st instar larvae show that most species in which the mandibles have acutely-angled narrow denticles, also have a large medial comb on the inner surface. These imitate "flanges" on separate denticles (Figs 9, 15, 16).

Retinaculum. The mandibles of Notodontidae have a retinaculum located on the oral surface. My investigations show that the retinaculum is not yet formed in the 1st instar, except in the highly specialized genera *Stauropus* and *Cnethodonta*, where it is distinct but not sclerotized (Figs 3, 4).

Dockter (1993) noted the presence of a retinaculum in the 2nd instar for two species of *Heterocampa* Doubleday from North America. The Palaearctic species I studied have a

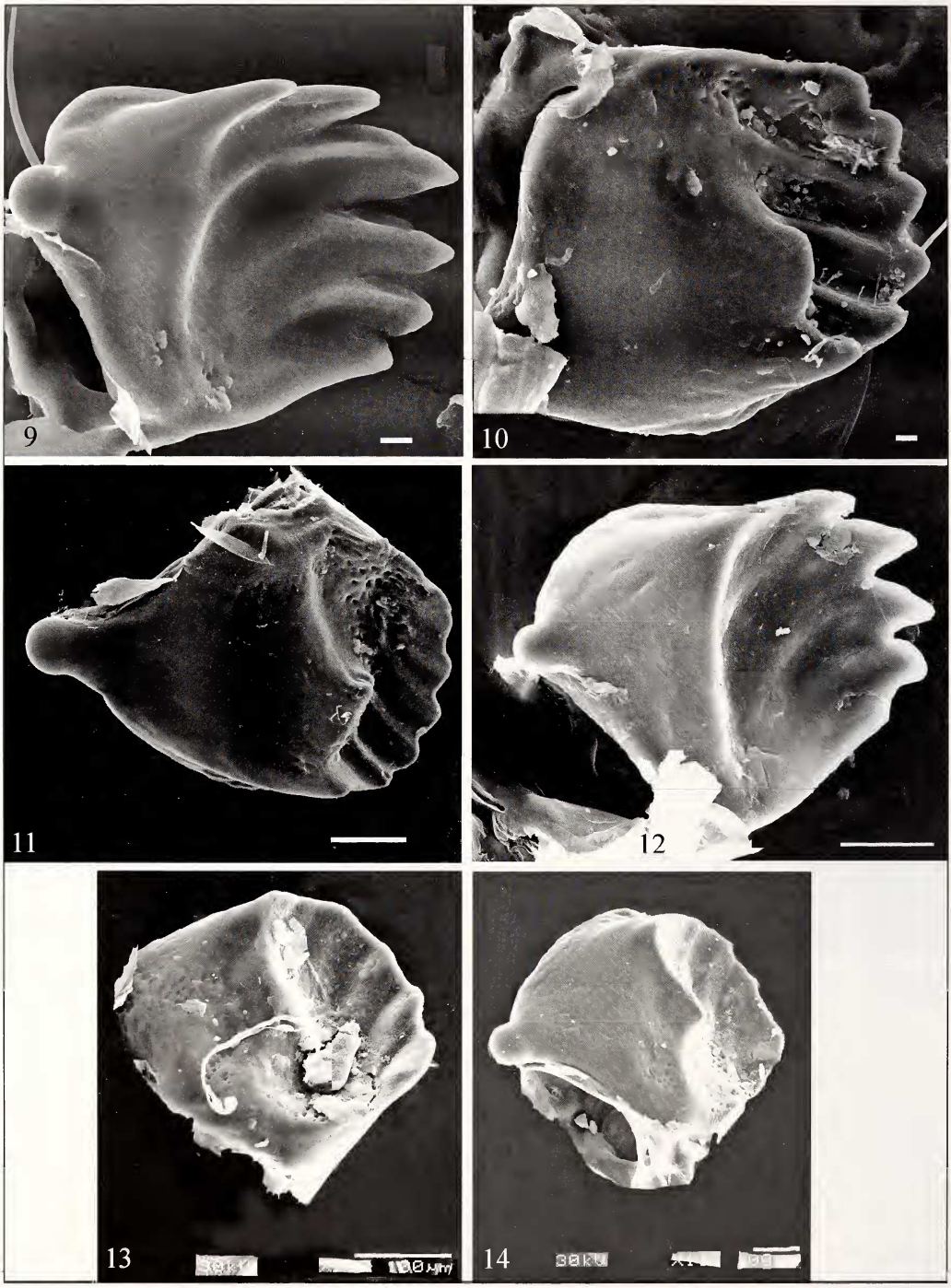


Figs 5–8. Oral surface of right mandible of Notodontidae larvae. **5.** 4th instar *Gonoclostera timoniorum* (220 ×). **6.** 1st instar *Clostera anachoreta* (480 ×). **7.** 1st instar *Pygaera timon* (600 ×). **8.** 2nd instar *Pygaera timon* (430 ×).

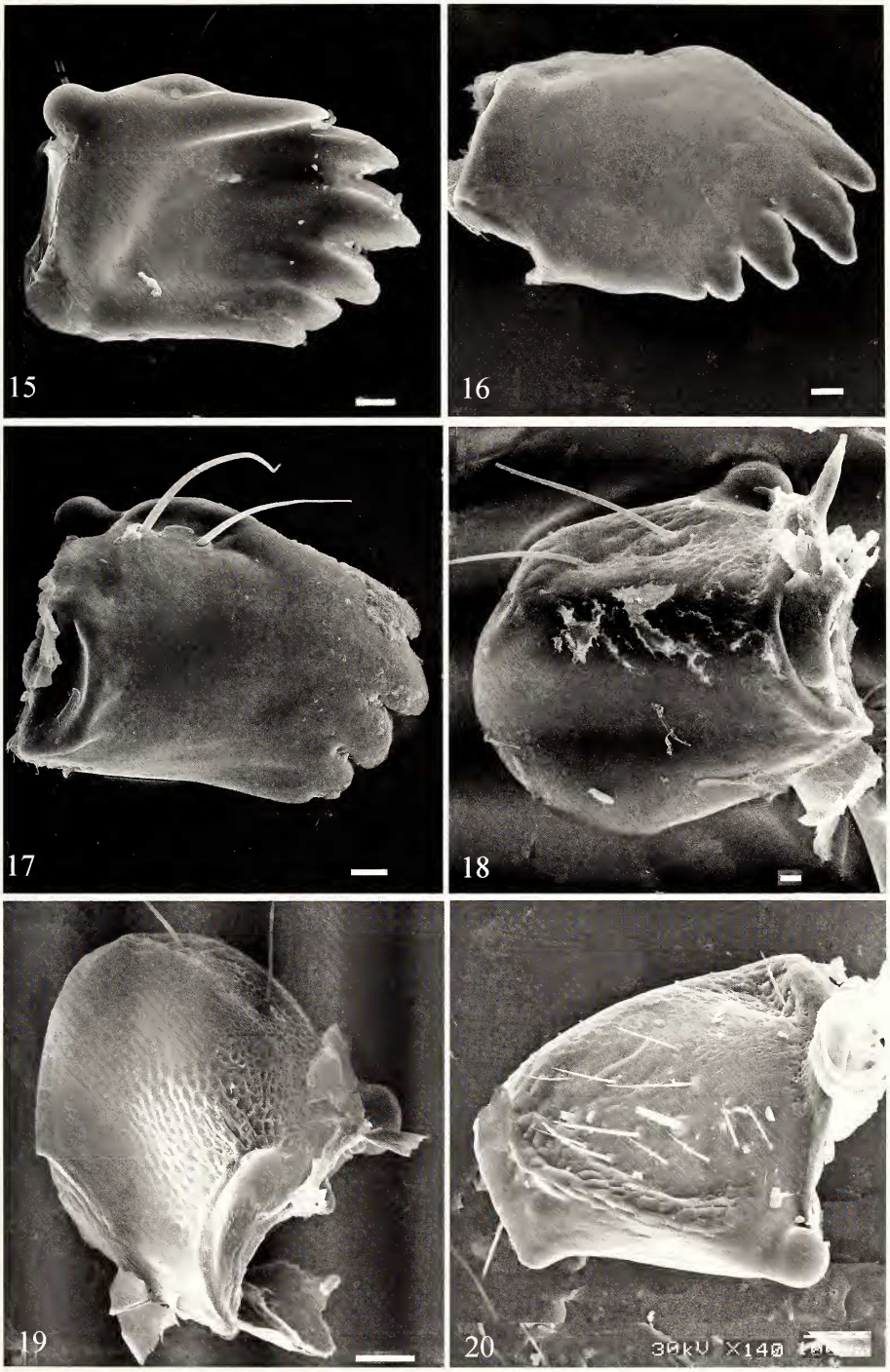
well sclerotized retinaculum in the 2nd instar which becomes more heavily sclerotized in the 4th and 5th instars, thus providing additional strength for the mandibular cutting edge. Rarely the retinaculum appears not in the 2nd but in the 3rd instar (*Dicranura)* and even in the 4th (*Pygaera*).

The retinaculum may be flattened (*Pterostona, Micromelalopha*, *Gonoclostera*, and others, Fig. 5), with a small projection (*Semidonta, Euhampsonia* and others), or with a large, high comb (*Uropyia, Dicranura, Nerice*, Figs 11, 14), which increases in the 3rd and 4th instars.

Mandibular carina. The presence of a mandibular carina and its disposition on the ventrolateral mandibular surface of some species of Notodontidae has been noted by Miller (1991: 124, 125, Figs 395–397). My studies show that this structure looks like a



Figs 9–14. Oral surface of mandibles of Notodontidae larvae. **9–11.** *Nerice davidi* (right mandible). **9.** 1st instar (660 ×). **10.** 2nd instar (440 ×). **11.** 3rd instar (160 ×). **12–14.** *Dicranura ulmi*. **12.** 2nd instar (right mandible, 450 ×). **13.** 3rd instar (left mandible, 230 ×). **14.** 4th instar (right mandible, 110 ×).



Figs 15–20. Surface of mandibles of Notodontidae larvae. **15.** Oral surface of right mandible of 1st instar *Clostera pigra* (660 ×). **16.** Lateral surface of left mandible of 1st instar *Furcula bifida* (600 ×). **17.** Lateral surface of left mandible of 1st instar *Notodonta torva* (780 ×). **18.** Part of mandibular carina (above side) of right mandible of 2nd instar *Spatalia dives* (440 ×). **19.** Part of mandibular carina (above side) of right mandible of 4th instar *Uropyia meticulodina*. **20.** Ventrolateral surface (area limited by mandibular carina) of left mandible of 4th instar *Dicranura ulmi* (140 ×).

comb, limited to the ventrolateral surface of the mandible (see Fig. 20). Most genera of Notodontidae have a more or less developed carina (Figs 17–20) and only some have a clearly expressed carina (*Dicranura*, *Phalera, Nerice*, *Clostera*, and others). This character is difficult for taxonomic interpretation.

Mandibles with secondary setae. Gardner (1943) and Miller (1991) noted the presence of secondary setae on the mandibles of Thaumetopoeinae. I found secondary setae on the mandibles in 4th and 5th instar larvae of *Dicranura* (Fig. 20), but nowhere else among the taxa studied.

Discussion

The classification of the Notodontidae is in dire need of improvement. In the systems proposed by different authors an uncertainty about the number of subfamilies as well as the classification of their genera remains until now. The recent classifications of the Notodontidae (Tikhomirov 1981; Schintlmeister 1985; Miller 1991) have the best argumentations. Now I want to show how the results of my original investigations agree or disagree with the above-mentioned classifications.

The larval mandibles of the majority of the investigated genera of Notodontidae are uniform. Their mandibular margin possesses 6 acutely-angled denticles in the first instar, which then becomes smooth in the 2nd through 5th instars. Such structure is present in 21 genera, namely *Euhampsonia, Furcula, Uropyia, Harpyia, Fentonia, Drymonia, Notodonta, Peridea, Semidonta, Leucodonta, Lophocosma, Pheosiopsis, Shaka, Pterostoma, Ptilodon, Lophontosia, Hagapteryx, Allodonta, Hexafrenum, Epodonta*, and *Spatalia*. In this case my data are mostly coordinated with the system of Tikhomirov (1981) where these genera, except *Furcula* are included into subfamily Notodontinae.

Genus *Furcula* in the classifications of Tikhomirov (1981) and Schintlmeister (1985) is placed in the derived subfamily Cerurinae. On the other hand, Miller (1991) transferred this genus to subfamily Notodontinae, in tribe Dicranurini. My data of the larval mandible structure do not contradict this opinion.

The placement of genus *Harpyia* in the Notodontinae by Tikhomirov (1981) is supported by characters of the structure of the larval mandibles whereas other peculiarities of the larva, egg, and pupa characterize this genus as highly specialized (Dolinskaya 1986, 1987 a, c; Dolinskaya & Plushch 2003), which is reflected in the classifications proposed by Schintlmeister (1985) and Miller (1991). The first author placed this genus into subfamily Stauropinae while the second included it into the Heterocampinae, Stauropini.

Genera *Pheosia* and *Phalera* as well as the above-mentioned 21 genera are characterized by mandibles with 6 acutely-angled denticles in the first instar; however, they are not narrow and acute, but broad and fllattened. Tikhomirov (1981) included both genera into subfamily Notodontinae and noted that *Pheosia* is characterized by the highest specialization among the Notodontinae. The genus is characterized also by a rather specialized sculpture of the egg chorion (Dolinskaya 1987 b, c). The taxonomic position of the genus is intended to be investigated further. There are two opinions concerning the position of genus *Phalera* in the notodontid classification. Tikhomirov (1981) consid-

ers that it must be included within the Notodontinae while the other authors suggested that it belongs to the Phalerinae (Schintlmeister 1985; Miller 1991).

Genera *Stauropus* and *Cnethodonta* have flattened, broad mandibles with 4 denticles in the 1st instar. I consider this state to be apomorphic because most representatives of the outgroup (Noctuidae, Lymantriidae, Arctiidae) have the mandibular edge with 5–6 acutely-angled, narrow denticles in the 1st instar. Besides, these genera have a retinaculum in the 1st instar. In this case my conclusions are consistant with those of the other authors. Miller (1991) included these two genera into the Heterocampinae, Stauropini, while Schintlmeister (1985) and Tikhomirov (1981) placed only genus *Stauropus* into their Stauropinae. Tikhomirov (1981), based on characters of the functional morphology of the genitalia retains *Cnethodonta* in the less advanced Notodontinae, i.e. *Cnethodonta* is regarded by him as the less advanced genus relative to *Stauropus*, and this fact is also corroborated here (the denticles of the 1st instar larvae are less flattened).

In genera *Clostera, Gonoclostera, Pygaera, Micromelalopha, Gluphisia, Dicranura*, and *Nerice*, as opposed to the other notodontid larvae, the serrate mandibles do not disappear in the 2nd instar and there is a smooth process of their transformation to the last instar. I consider such state to be plesiomorphic because of the presence of mandibular denticles in 1–5th instars in most representatives of the outgroup. The mandibular margin becomes smooth in the 3rd instar in *Clostera, Gonoclostera, Pygaera, Micromelalopha*, and *Gluphisia*. In the 4th instar of *Dicranura* the mandibular edge becomes sinuous. In *Nerice* the mandibular edge looks like 6 fused distinct denticles until the 5th instar. The above-mentioned genera have common characters as well as specific peculiarities.

For example, *Clostera, Pygaera, Micromelalopha, Dicranura*, and *Nerice* have a well expressed carina. In *Gonoclostera* and *Gluphisia* the mandibular carina is weakly expressed. *Pygaera*, *Gluphisia,* and *Dicranura* may be united by the absence of the retinaculum in the 2nd instar, whereas in the rest of the genera this structure is present. Besides that, *Clostera, Pygaera*, and *Micromelalopha* have the retinaculum with only a small projection while *Dicranura* and *Nerice* have a large, high comb. In addition, *Dicranura* have secondary setae on the mandibles in the 4th and 5th instars.

Concerning genera *Clostera, Gonoclostera, Pygaera*, and *Micromelalopha* my data coincide with the classifications of the three above-mentioned authors. In the classifications of Tikhomirov(1981) and Schintlmeister (1985) these genera are included into the primitive subfamily Pygaerinae. Miller (1991) placed into this subfamily only genus *Clostera* and said that following further investigation genera *Micromelalopha, Pygaera*, and *Gonoclostera* perhaps will be included into Pygaerinae also. It must be noted that the mandibular denticles of *Micromelalopha* in the 2nd instar are rather broadened, flattened, and rounded in comparison with those of *Clostera, Gonoclostera*, and *Pygaera*. I consider this state of the denticles to represent an apomorphy for this genus.

Gluphisia requires additional research. The peculiarities of the mandibles and pupa (Dolinskaya 1986, 1989) show similarities with genus *Clostera, Gonoclostera, Pygaera*, and *Micromelalopha*. The data that I obtained do not match with any of the published classifications. Packard (1895) placed *Gluphisia* into the separate subfamily Gluphisiinae; Tikhomirov (1981) and Miller (1991) into subfamily Notodontinae.

Schintlmeister (1985) placed *Dicranura* into the derived Stauropinae together with *Harpyia* and *Stauropus*. The results of my studies are not concordant with this point of view. I consider that *Dicranura* has a complex of primitive attributes that are characterictic of the Pygaerinae and Thaumetopoeinae, as well as a complex of specialized features that are characteristic only to the genus. Thus, it is necessary to undertake more detailed investigations.

The position of genus *Nerice* in the Notodontidae remains unclear. Among all known classifications its status is discussed only by Packard (1895) and Tikhomirov (1981) who include it into the Notodontinae.

Summarizing the above-discussed characters of the Notodontidae it can be concluded that the morphology of the larval mandibles allows to unravel related groups within the family. The genera with more specialized morphology, as a rule, possess apomorphic states of the mandibular characters. However, the reconstruction of the Notodontidae phylogeny is not the main goal of the present paper, and a well-argumented classification should be based on a phylogenetic analysis involving a complex of characters, including larval, but also characters of the eggs, pupae, and imagos.

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